

## THE NEED FOR INTEGRATED STUDIES OF THE CALIFORNIA FLORA

BRENT D. MISHLER

Jepson Herbarium, University Herbarium, and Department of Integrative Biology,  
University of California, Berkeley, CA 94720-2465

### ABSTRACT

The general field of systematic biology is an inclusive discipline that has taken great steps forward in the last two decades. New theories and methods have been developed for using character data to reconstruct phylogenetic relationships and thus improve classifications. Copious new sources of character data have become available from the molecular level. New analytical methods have been developed for using phylogenies to quantify biogeographic, ecological, and evolutionary patterns and test hypotheses about process. These new developments need to be integrated with traditional strengths in systematics such as collections-based research, floristics, and morphological/developmental studies, through greater communication and collaboration. Because of its unique geology and biology, its long and intense history of study, and its outstanding botanical institutions, California can serve as an ideal model for a newly integrated approach to systematic biology.

There is a danger, in this time of specialization and information overload, to become too narrowly entrenched in one's main activities. This happens in the botanical community of California: an in-the-trenches conservationist can get frustrated with an herbarium researcher because of taxonomic name changes that may on the surface seem aggravating and pointless. A consultant doing field inventories might not see the need for all the theory and heavy-duty computation applied in academic ecology these days. A systematist comfortable with morphological characters in a large part of the flora might be suspicious of the proliferation of molecular characters and cladograms. A molecular systematist might lose touch with the important morphological characters that should be useful for their work. Some professors in academia may get too far removed from the realities and training needs in the outside botanical community. The list could go on, but I hope the main take-home message is clear: we need some mutual enlightenment and understanding.

The study of plant systematics and evolution is an integrated whole. We need the floristic specialists with their good field knowledge of geography and variation in plants. We need to add molecular characters to the mix, while not losing the ability to gather, evaluate, and use morphological and anatomical characters. We need a strong, well-justified theoretical framework within which to test hypotheses. We need the powerful new analytic tools available in ecology and systematics to look at community structure and phylogenetic trees in more sophisticated ways. And most of all, we need to develop the best understanding we can of the flora at all levels, communicate it clearly to the relevant communities, and apply it to the urgent conservation needs facing California (see also Baldwin 2000). Thanks to Jepson's foresight in creating a practical botanical institution in the center of an

academic hotbed, the Jepson Herbarium is perfectly placed to span these different approaches and encourage much needed integrated studies, which we attempted to do with this symposium.

The field of systematic biology has taken great steps forward in the last two decades, in three major areas. One major step forward has come about through the introduction of new theories and methods for using character data to reconstruct phylogenetic relationships and thus improve classifications. The second major step forward was the introduction of copious new sources of character data from the molecular level. The third major step forward was in the development of analytical methods to use phylogenies to quantify biogeographic, ecological, and evolutionary patterns and test hypotheses about process. I will go into each of these new developments in turn, with the goal being to show how they can be integrated with traditional strengths in systematics such as collections-based research, floristics, and morphological/developmental studies to yield a truly integrated approach.

### Phylogenetic Systematics

*The need for phylogenetic classification.* The main developments in systematic theory stem from the phylogenetic approach developed by Hennig (1966). I summarized the new developments in *Madroño* in 1995, and they have been well outlined elsewhere in texts and reviews (Farris 1983; Sober 1988; Forey et al. 1992; Maddison and Maddison 1992; Mishler 1994, 2000). A quick outline should thus suffice here: the fundamental idea is that phylogenetic branching events among lineages should be reconstructed using shared, homologous *markers* (Mishler 2000). The markers are characters that changed state along a lineage, thus serving as evidence in the future that the lineage once existed. The derived state of a marker when shared among

contemporaneous taxa (called a synapomorphy) can thus be used to postulate the existence of a once-shared lineage uniting them. This hypothesis can be tested by other putative synapomorphies, and so on. In Hennigian systematics, classification follows the reconstruction of a well-supported phylogeny, and only hypothesized monophyletic groups should be named—these are groups that consist of all and only descendents of a common ancestor. Thus in current thinking there is a fundamental isomorphism among synapomorphy, monophyly, and named taxa.

Why has this three-fold parallelism been so widely accepted across the community? Phylogenetic classifications may not always be the most practical, that is the synapomorphic characteristics may sometimes be hard to detect easily. There is an element of human choice in what we use our formal Linnaean nomenclatorial system for, so why choose phylogeny as a basis? To answer this question requires an examination of what classifications are for. Evolution is real, as are organisms (physiological units), lineages (phylogenetic units), and demes (interbreeding units), for example. On the other hand, our classification systems are obviously human constructs, meant to serve certain purposes of our own: communication, data storage and retrieval, predictivity, and studies of process. While the last purpose seems perhaps the most esoteric, the most important function of a classification is its theoretical meaning, as discussed by Mishler (2000). A classification should capture units participating in the most important causal processes operating in the system. In this way the classification will be maximally predictive and useful for practical and theoretical purposes. In biology, our best understanding is that evolution is the most important process organizing biological diversity, and thus the field of systematics in general has settled on restricting the use of formal taxonomic names to represent phylogenetically natural, monophyletic groups. While this is a widely understood standard for modern systematics, recent developments in two areas deserve further, more detailed, discussion: species concepts and rank-free classification.

*Species.* Given the above arguments, what should the species rank represent in the Linnaean classification system? There are two necessary parts to any species definition. The criteria by which organisms are *grouped* into taxa must be specified, as well as the criteria by which a taxon is *ranked* as a species rather than some other hierarchical level. Following the arguments given above supporting a Hennigian phylogenetic system of classification in general, the *grouping* criterion that should be used at the species level, as at all other levels, is monophyly (Mishler and Theriot 2000). Under this view, apomorphies are considered to be the necessary empirical evidence for unambiguous phylogenetic species, as for phylogenetic taxa of all ranks. It follows that re-

productive criteria cannot be used to group organisms into phylogenetic species. The fundamental inappropriateness of using breeding compatibility in cladistic analysis is because the ability to interbreed (potential or actual) is a symplesiomorphy (i.e., shared primitive characteristic) by definition, thus not a phylogenetically valid grouping criterion. The species *ranking* decision is currently forced because systematists have legislatively constrained themselves to use a ranked Linnaean hierarchy (see the following section for a possible alternative). The ranking criteria for species should involve practical criteria such as the amount of character support for a group; the species could then be viewed as the smallest hypothesized monophyletic group with good support (the minimum-rank taxon—see Baldwin 2000, this issue). The species ranking decision may also involve biological criteria in better known organisms, including reproductive criteria, e.g., the origin of a distinctive mating system at a particular node or the acquisition of *exclusivity* (a condition in which each allele in a lineage is more closely related to another allele in the lineage than it is to an allele outside the lineage; Baum and Shaw 1995; Graybeal 1995).

There are, of course, difficulties applying the concept of monophyly at this level. There are a number of different sources of homoplasy (incongruence between certain character distributions and the cladogram based on maximum parsimony), such as adaptive convergence, gene conversion, developmental constraints, mistaken coding, lineage sorting, reticulation, etc. The last named factor is the most problematical because it involves the fundamental model of reality underlying cladistic analysis—the other factors are cases of mistaken hypotheses of homology, whereas “homoplastic” character distributions due to reticulate evolution involve true homologies whose mode of transmission is not tree-like.

As less inclusive levels in the genealogical hierarchy are considered there is an increasing probability that reticulating (“hybridizing”) events will occur, rather than the diverging phylogenetic relationships assumed by the cladistic approach. However, the problem of reticulation is not confined to the species level; indeed, reticulation can occur throughout the hierarchy of life, and so is a problem of more general difficulty, and one that is receiving more attention by systematists (e.g., McDade 1990, 1992). It is becoming clear that while a certain amount of reticulation does not preclude cladistic reconstructions of phylogeny, extensive reticulation can cause major problems. We can reconstruct relationships in the face of *some* amount of reticulation (how much is not yet established, but is amenable to study, e.g., McDade 1992). As with convergence, where the application of cladistic analysis provides the only rigorous basis we have for identifying homoplasy and thus demonstrating non-parsimonious evolution, the only way we can identify

reticulation on the basis of character analysis alone is through the application of cladistic parsimony, followed by examination of homoplasy to attempt to discover its source (see discussion by Vrana and Wheeler 1992; Mishler and Theriot 2000). How modes of reticulation actually affect character distributions on cladograms is a productive avenue for empirical and theoretical investigations.

To summarize, a *phylogenetic species concept* (Mishler and Theriot 2000; not to be confused with the different phylogenetic species concepts of Cra-craft 1983; Nixon and Wheeler 1990) can be defined based on the following considerations. First, organisms should be grouped into taxa at all levels (including the lowest level, species) on the basis of evidence for monophyly; breeding criteria in particular are not useful for grouping purposes. Second, criteria used to assign species rank to certain monophyletic groups must vary among different organisms, but might well include ecological criteria or presence of breeding barriers in particular cases (see Mishler and Brandon 1987; Mishler and Theriot 2000 for elaboration).

*The need for rank-free classification.* The above discussion assumes that the current Linnaean system of ranked classifications is to remain in place, thus the species ranking decision is forced because systematists have constrained themselves to use a ranked Linnaean hierarchy. An intriguing possibility has arisen through recent suggestions for reforming the Linnaean system by removing the concept of ranks (De Queiroz and Gauthier 1992). This proposed change would keep the hierarchy of named phylogenetic groups, but remove the ranks (including species) associated with the names. This would remove the arbitrariness of ranking decisions at the "species level" (Mishler 1999).

As the community has applied phylogenetic analysis broadly at many levels, it has become clear that the ranks in the Linnaean system (orders, families, genera, etc.) are problematic for classification. The many changes that are needed to bring classification into line with our understanding of phylogeny, plus the sheer number of levels being resolved in the tree of life, have made the current system of nomenclature appear a bit outdated. There are not nearly enough ranks to suffice in classifying the tree of life, with its millions of branches.

Furthermore, there are practical problems with the use of ranks. Most aspects of the current code, including priority, revolve around the ranks, which leads to instability of usage. The need to maintain the hierarchy of the ranks leads to names being changed without good reason. For example, when a change in relationships is discovered, say a current family is found to be nested cladistically inside another family, several names often need to be changed to adjust, including the names of groups whose circumscription has not changed. Frivolous changes in names often occur under the current

code, when authors merely change the rank of a group without any change in postulated relationships at all.

The most important problem with ranked classifications are that they lead to bad science, if a user of a classification naively assumes that taxa at the same rank are comparable in some way. The existing, ranked Linnaean nomenclatorial system is based on a non-evolutionary world-view (with taxa at the same rank being somehow equivalent in the mind of the creator). Under an evolutionary world-view, the ranks don't make sense. Practicing systematists know that groups given the same rank across biology are not comparable in any way (i.e., in age, size, amount of divergence, diversity within, etc.), but many users of classifications do not know this. For example, ecologists or paleobiologists often count numbers of taxa at a particular rank as an erroneous measure of "biodiversity."

I have argued (Mishler 1999) that the formal ranks should be abandoned (including the species rank), for efficient and accurate representation of phylogenetic relationships. Instead, names of clades should be hierarchically nested uninomials regarded as proper names (although current usage should be followed as much as possible to retain links to the literature and collections). A clade should retain its name regardless of whether new knowledge might change its phylogenetic position, thus increasing nomenclatorial stability. Furthermore, since clade names would be presented to the community without attached ranks, users would be encouraged to look at the actual attributes of the clades they compare, thus improving research in comparative biology. In the future, I hope that "rank-free" phylogenetic taxonomy will allow efficient presentation of theoretically justified, maximally useful classifications that will unify biology by providing a single, consistent framework for the study of evolutionary and ecological processes at all levels.

#### Molecular Data

Many new data sets have been added to systematics because of the availability of technology from molecular biology that allows relatively easy comparative sequencing of genes (Soltis et al. 1998). It is important to note at the outset that these new molecular data are not meant to *replace* traditional morphological and anatomical characters in systematics. On the contrary, a number of recent studies in the field have shown that molecular characters, while a very useful addition to systematics, are *complementary* to the traditionally used characters. These new characters should be added to appropriate morphological characters and used to improve our knowledge of plant relationships, including species circumscriptions as well as relationships among species, genera, and families. In turn, improved understanding of relationships is necessary

to inform our practical uses of plants and our conservation efforts.

Various laboratory techniques have been developed for molecular systematic studies. Some of these, such as DNA hybridization and restriction fragment length polymorphisms (RFLPs) yield only distance information, which is difficult to apply to phylogenetic tree reconstruction since information about individual homologies is missing. Other techniques, including mapping of restriction enzyme sites and direct DNA sequencing methods, yield information about specific characters. The latter techniques are thus more heavily favored, because character-based methods (based on explicit evolutionary models of homology) provide markers suitable for phylogenetic analysis, as described above.

Speaking generally, molecular data do have a number of advantages for systematic studies (Mishler 1994). A large number of molecular characters is available for any given level of phylogenetic inference, which has proven to lead in many cases to increasingly better-supported hypotheses of relationships. This advantage seems particularly true at low taxonomic levels, even within species, where morphological characters tend to be subtle and hard to define. On the other hand, molecular data have some disadvantages as well. There are problems with sampling at the molecular level—it is time consuming and expensive to sample within study taxa (to check for polymorphism) at the level that is possible for many morphological characters, and, of course, fossil taxa generally cannot be included. Point mutations in DNA are simple characters with few possible character-states, subject to parallel changes that can't be detected easily except through their congruence with other characters on a cladogram.

Morphological characters have a number of advantages of their own (Mishler 1994). They are often complex in structure and development, with many possible character-states, thus allowing better supported initial hypotheses of homology. Sampling within study taxa to understand polymorphism is often easier and cheaper than with molecular data. Many key morphological characters can be seen in well-preserved fossils, thus allowing inclusion of completely extinct lineages, which can be essential to getting the correct tree. Morphological characters are, of course, subject to their own difficulties of interpretation, as compared to molecular data. There are usually many fewer characters, variation patterns can often be difficult to organize into discrete character-states, and convergence can lead to mistaken hypotheses of homology (of course, congruence can plague molecular characters as well).

The generalized strengths and weaknesses of molecular and morphological data are complementary to a large extent. Thus, the best approach, of course, is to apply appropriate characters from all levels of organization to some specific problem of

relationships. Molecular characters will remain essential as the bulk of available evidence, particularly for shallower branching events. Morphological characters will also remain critical pieces of evidence for many branch points in evolutionary history, particularly the deeper ones; plus they are essential for integrating fossils into evolutionary trees and of course for identification purposes in practical applications of systematics such as floristics. Thus, the future clearly lies in studies integrating both sources of data.

### Comparative Biology

The interplay and contrast between phylogenetic and functional/structural groupings has ushered in a new era of scientific rigor in comparative biology with the development of explicit and testable hypotheses of phylogenetic relationships. Many advances have been made in improving evolutionary model building as a route to understanding; "tree-thinking" is now central to all areas of systematics and evolution. The central importance of phylogeny reconstruction in systematics, ecology, and evolutionary biology has become widely realized in recent years (Donoghue 1989; Funk and Brooks 1990; Wanntorp et al. 1990; Brooks and McLennan 1991; Harvey and Pagel 1991; Miles and Dunham 1993; Martins 1996). Explicit cladistic phylogenies now provide a critical basis for classification as well as for studies of speciation, biogeography, ecology, and behavior (among many other areas).

The area of phylogenetic comparative methods is one of considerable controversy and rapid conceptual development. Virtually every issue of major journals and each new book on systematics and evolution contains something of interest on this subject. The general working procedure is to first carefully define the causal hypothesis to be tested, then specify a null hypothesis (what you would expect if the hypothesized cause is not working), and finally design a phylogenetic test that would let you reject the null hypothesis if it is indeed false.

The large number of comparative methods can best be summarized by placing them into categories corresponding to the types of hypotheses meant to be tested, as addressed below.

*Comparing cladograms.* These methods are meant for comparing different phylogenetic trees in the study of *coevolution*. Coevolution can be broadly defined as congruence between two or more systems undergoing tree-like evolution (i.e., evolution by descent with modification). This is a generalization of the phylogeny/homology relationship (i.e., the "coevolution" of organism lineages and characters discussed above). Coevolution comes in many forms: vicariance biogeography (organism/earth coevolution), host/parasite relationships, community evolution (e.g., symbionts, pollinator/plant coevolution, or other long-term ecological associations).

Biogeography can serve as an example of the concept of comparing trees for their mutual information content. Historical biogeography has a long tradition in biology, and was indeed a major source of evidence for Darwin. After evolution became widely established as a principle, the initial approach to biogeography was to look for areas of origin and dispersal patterns based on stable world geography (see Wiley 1981). The work of Hennig (1966) led to the development of *phylogenetic biogeography*, which examined the distribution of one group at a time in relation to a cladogram. One famous outcome was Hennig's "progression rule," the observation that more derived species often tend to occur further from the initial area of a lineage following speciation by peripheral isolation. The phylogenetic examination of many groups at a time can be traced to the works of Croizot following a method he called "panbiogeography"—a search for generalized distributional "tracks." This search for matching geographic patterns led to the approach called *vicariance biogeography*, a search for sister groups sharing the same pattern across many cladograms (Nelson and Platnick 1981).

The basic idea is to look for common patterns (and causes) of distribution—evidence from other organismal distributions can be relevant to understanding the distribution of a particular group! Congruence is taken as evidence of shared biogeographic history (vicariance); incongruence as evidence of separate history (dispersal). Methodologies have diversified to compare cladograms in coevolutionary studies, including consensus techniques (Funk and Brooks 1990), tree-to-tree distance metrics (Penny and Henny 1985), and parsimony techniques (such as Brooks parsimony; see Brooks 1990; Brooks and McLennan 1991).

*Comparing clades within a cladogram.* These methods are meant to detect whether there are imbalances in symmetry between sister clades in the same cladogram, in order to address various questions in both micro- and macro-evolution. First of all, however, what is the null expectation? Intuitively, one might expect balanced trees, perhaps, based on some sort of false analogy to coin flips. But is this a correct assumption? "Random" trees can be generated in many ways (Maddison and Maddison 1992), and include equiprobable trees (picked out of a set of all possible trees—bias towards asymmetry), random joining trees (models a random speciation process—intermediate bias), or a random partition (bias towards symmetry). Using a Yule "pure birth" Markovian model to grow random trees, Slowinski and Guyer (1989) showed a non-intuitive result: the probability of each way of partitioning taxa at a bifurcating node is equal [for  $n$  terminal taxa, the probability of generating any division of species above a node into sister lineages of unequal size is  $2/(n - 1)$ ; the probability is  $1/(n - 1)$  for evenly divided sister lineages]. Thus, even

a node in which one species is the sister taxon to 39 other species is not significantly unbalanced at the  $P = 0.05$  level ( $P > 0.051$ ).

This work has led to the realization that real trees should be expected to be quite asymmetrical even under a random model. Furthermore, even if trees are judged significantly asymmetric, how can we associate that judgement with some specific factor postulated to be the cause of that asymmetry? That leads to the hot topics of "key innovations" and "adaptive radiations." There have been many, often conflicting definitions of *adaptive radiations* (Givnish and Sytsma 1997). Decomposing the term is best, and suggests that "adaptation" needs to be established separately from "radiation." The rapid diversification of lineages (caused by a postulated "key innovation") should be accompanied by ecological, morphological, and/or genetic diversification. A number of methods have been developed to deal with the required time estimation problem, which involves two questions: Can we assume a molecular clock? If we can, how do we calibrate it (Sanderson and Wojciechowski 1996; Sanderson 1997; Baldwin and Sanderson 1998)?

*Discrete-state character comparisons on a cladogram.* These methods are meant for examining how discrete-state characters evolve on a tree individually and together. Such characters can be mapped onto cladograms using parsimony, so as to minimize the number of character-state changes. In this way, suites of characters are built up for Hypothetical Taxonomic Units (HTU's). Specific types of hypotheses that can be tested include polarity of character-state changes in one character, and the association of state changes in two characters, either undirected (Ridley's test; Ridley 1983) or directed (Maddison's test; Maddison and Maddison 1992).

Most of these studies are motivated by the search for *adaptation*. There is a long-standing observation that organisms tend to match their environment. Darwin and many Darwinians thought that all structures must be adaptive for something. But this assumption has come under severe challenge in recent years (Gould and Lewontin 1979). Not all structures and functions are adaptive. In fact, there are very few completely demonstrated examples of adaptations.

The definition of adaptation in a formal sense requires fulfillment of four different criteria (Mishler 1988; Brandon 1990):

1. Engineering. Structure must indeed function in hypothesized sense. Requires functional tests.
2. Heritability. Differences between organisms must be passed on to offspring, at least probabilistically. Requires heritability tests (parent-offspring correlations; common garden studies).
3. Natural Selection. Difference in fitness must occur because of differences in possession of the hypothesized adaptation in a common environment. Requires fitness tests.

4. Phylogeny. Hypothesized adaptive state must have evolved in the context of the hypothesized cause. Requires phylogenetic tests.

Only something that passes all these tests is an *adaptation*. If it passes tests 1–3, it can be called an *aptation*. If it then fails test 4 it can be called an *exaptation* (Gould and Vrba 1982). Thus, a phylogenetic test, while not sufficient in itself, is necessary as part of a complete adaptive explanation (Coddington 1988; Mishler 1988; Donoghue 1989).

*Continuous character comparisons on a cladogram.* These methods are meant for examining how quantitatively varying characters are associated on phylogenies. Note that these are characters that do not meet the ‘discrete-state’ criteria for taxonomic characters. The “bad old way” to compare two such characters was through direct correlations of species values (using species as data points). However, as pointed out by Felsenstein (1985) and others, this treats species as if they are all equally related to each other. The advent of quantitative comparative approaches was motivated by attempting to “remove” the influence of history, for example using ANOVA and ANCOVA (Harvey and Pagel 1991), autocorrelation (Cheverud and Dow 1985), independent contrasts (Felsenstein 1985; Burt 1989), and general linear model approaches to partition variance and “subtract” the phylogenetic effects (Martins 1996). Conversely, other methods explicitly describe variation due to phylogeny by tracing the quantitative characters on a phylogenetic tree, reconstructing values for nodes, and looking at direction of change by comparing ancestors and descendants (e.g., Huey and Bennett 1987).

### The Integrative Approach

These diverse sources of data, complex theories, mathematically complicated algorithms, and multiple approaches to analysis have reinvigorated the field of plant systematics, yet at the same time they have made the field more complex and harder to master. No one person can keep ahead of all these parts of the whole endeavor. Thus, there will be an increasing need for mutual understanding among specialists, increased collaborative research, and more sharing of expertise. Training of students must continue to diversify into all the new approaches, while at the same time not losing sight of older, still valuable approaches. Botanical institutions need to adapt and expand their vision and capabilities. Our ultimate goal for the next 50 years of California botany should be to serve as a model by developing integrated studies that combine all these approaches and presenting this information in easily accessible ways to the public.

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